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OBSERVATIONS UPON THE HABITS, STRUCTURE AND DEVELOPMENT OF AMPHIOXUS LANCEOLATUS.

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[*Concluded from the January number.*]

Nervous System.—This system consists of a central and a peripheral portion. The central portion, or *chorda spinalis*, is a long, slender, slightly tapering body, nearly round in section, and extends from the posterior to within a short distance of the anterior extremity of the dorsal aspect of the notochord. The anterior end is somewhat larger, for a short distance, than the rest of the chorda, and forms a sort of elongated head with a short, pointed, beak-like termination, which lies close upon the notochord. Upon the left side of this "head," and near the end or anterior portion, there is a slight cone-like projection, which is in close proximity to and points towards the ciliated pit or depression of the left side of the body. This projection is considered to represent a single olfactory nerve or lobe, and if the pit is indeed a nasal fosse, then undoubtedly this protuberance is an olfactory organ. With the exception of this nerve or lobe this end of the chorda does not present the slightest indication of the divisions or lobes which form the brain of all other vertebrates.

The posterior extremity of the chorda makes a short upward bend, at nearly right angles to its former direction, and expands just above the end of the notochord, into a small, button-like termination, which probably through some accident in finishing the plate, is not shown in the figure of the adult animal. Between the two ends and along the center of the chorda there extends a narrow canal, which is of considerable size in the head portion, where it is enclosed by the anterior walls, but gradually diminishes in calibre towards the posterior extremity, where it is represented by the merest traces of a cleft or opening, as seen in the center of the "button" of this end.

The sides of this canal, throughout its entire length, are marked by small, black, roundish pigment spots, which are sometimes aggregated into small clusters, but more commonly are scattered along at varying intervals from each other. In the substance of the anterior, beak-like extremity, and just in front of the end of the central canal, there is a large pigment spot which is generally thought to represent the rudiments of a median eye; but if it does not, then Amphioxus is entirely lacking in such an organ. Prof. Quatrefages, in 1845,[1] described and figured a prominent protuberance as existing upon the side of the cord at this end, and claimed that it showed at its extremity a distinct and rather well-developed crystalline lens, thus representing a stalked eye, with the stalk pointing towards the anterior extremity of the body; but later observers have failed to confirm his observations in this respect, the only short protuberance which is formed along this portion being considered as representing, as already mentioned, an olfactory rather than an optic organ.

The peripheral portion of the nervous system consists of a succession of pairs of nerves given off from the upper part of the sides of the chorda dorsalis along its entire length. They originate in single roots, and arise at intervals corresponding to the divisions between each two of the muscle plates. With the exception of the first and last pairs, all the nerves are of nearly uniform size, and, with the same exceptions, they pass outward and downward branching two or three times in their course, to be distributed along the middle and lower portions of the sides of the body. Besides the lower branches, each of these nerves sends off, at a short distance from its origin, a branch which proceeds upwards to the dorsum of the animal, Fig. 6, Pl. II. The nerves, which form the first pair, arise anterior to the body muscles and from the anterior portion of the head of the chorda. They are quite large at their bases, and extend straight forward from the sides of the chorda towards the anterior end of the body, dividing in their course into a large number of branches which are distributed above and below, and all about the extremity of the notochord. These branches terminate, or at least many of them do, in the cells of the exoderm, or else in small bell-like knobs which are wedged in among the exodermic cells, and resemble them very much in shape and appearance. The last pair of nerves which arise at some distance from the end of the chorda, are directed backwards and perform the same offices for the posterior end of the notochord and the tail, that the first pair do for the opposite extremity, but the nerves themselves are not so large, being slightly larger than the ordinary body nerves, and they do not divide into nearly as many branches.

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[1] Annales des Sciences Naturelles. 3me série, Zoologie. Tome 4me, pp. 197–248, pls. 10–13, 8vo Paris, 1845.

Muscular System.—The muscular system may be considered as made up of two sets of body muscles; two sets of transverse abdominal muscles; few or many longitudinal fibres in and along the abdominal walls; mouth muscles; pharyngeal ring muscles, and sphincters for the mouth, branchiopore and perhaps for the ring or neck of the pharynx.

The *body muscles* are disposed as in ordinary fishes, one set upon either side and each set is composed of a series of regular, overlapping muscle plates, which extend from near the anterior extremity of the chorda dorsalis to within a short distance of its posterior termination. Along the entire length of their dorsal half, the two sets are either united or very closely approximated, and enclose the greater portion of the entire length of the chorda and of the notochord, but leave the extremities of both entirely bare of muscular covering (Fig. 1, Pl. 1). These muscles are also united along the ventral edge of the tail portion, but for the anterior two-thirds or more of their length their ventral edges are quite widely separated, spreading outward and downward from the notochord to form the upper portion of the parietes of the abdomen. The general outline of these combined plates, when seen from the side, is that of a long, slender spindle, gradually tapering from the center to a sharply pointed termination at either end. Each plate is composed of longitudinal, striped, muscular fibres, and is four-sided in outline, but with the greater diameter changing in direction according to the position of the individual plate along the side of the body. Those plates which are near either end are nearly rhomboidal in outline, long and narrow, and with the longer points coincident in direction with the notochord. Nearer the center of the body the plates are almost square, the diameters being nearly equal; while along the middle third, where they become once more rhomboidal, or nearly so, the longer diameter is at right angles to the notochord, with the longer portion of each plate running down into the abdominal walls. On account of the overlapping of each plate by the one immediately posterior to it, this foursidedness can be seen only in the last plate, which is entirely uncovered. These muscles give to the body whatsoever of color it may possess, and probably also its metallic iridescence, although this latter feature may be due to the striæ and fibres which exist in the integument. These muscles, from their very great extent as compared with the entire body, also give Amphioxus its remarkable power and activity in the sand and water, and from their similarity of arrangement at either extremity, enable, or rather compel it to move with that beautiful, elastic, line-of-beauty motion which is such an interesting feature of its progress. The *transverse muscles* lie in the walls of the abdomen and extend from the ventral edges of the muscle plates of either side to meet and unite in a raphe upon the median ventral line of the branchial sack. These muscles are nearly transparent in structure, and by their action serve to close the sack walls upon or towards the pharynx, as in the expulsion of water from the branchium by the branchiopore, and as is seen in all hardened or preserved specimens. The *longitudinal abdominal muscles*, which are found chiefly in the lower and posterior portion of the abdomen, probably assist in the contraction of the abdominal walls, and also serve to shorten the sack and open the branchiopore. The *mouth muscles*, arranged in the walls of the buccal cavity and attached to the mouth ring and its appendages, serve to open the mouth, and by this operation unclose the overlapping oral tentacles. It has been said that besides these general muscles there are special muscles which serve to move each individual tentacle separate from the entire circlet. I have never seen any evidence of any such muscles, and never, in a single instance any individual motion of the tentacles, and if such muscles exist their action must be very feeble or entirely nugatory. The *muscles* of the *pharyngeal ring* are situated in the posterior portion of the buccal cavity and attached to the borders of the ring so as to bring the tentacles of these parts forward across the mouth of the pharynx. The *sphincter muscles* surround their respective orifices and serve, as in the case of all sphincters, to approximate the edges of these different apertures. There may be a rudimentary sphincter to the anus, but neither in the young nor the adult have I ever observed what may be strictly called a closure of this orifice.

Reproductive Organs.—These organs consist of a number of roundish or oval bodies formed inside the lining membrane of the walls of the branchium and attached to the ventral edges of the muscle plates in a single row, along either side of the animal. Each body consists of a case or capsule enclosing a central solid portion or matrix, within which are developed the generative products, and each case is placed with the center of its upper border in juxtaposition to the line of overlapping or junction of two of the muscle plates (Fig. 6 *a*, Pl. II). Ordinarily these cases are small and inconspicuous, and lie entirely below the outline of the body muscles, but in the female, towards the breeding season, the ova increase so much in size that the cases become large and noticeable, closely pressed together, and extend for about a quarter or third of their diameter above the edge of the muscles to which they are attached, thus occupying a goodly share of the sides of the branchium. In the female which was in my possession there were twenty-six of these cases upon each side, extending from a little in front of the middle of the pharynx back to very near the branchiopore. In the males there were respectively twenty-three and twenty-five pairs of cases so that it is probable that there is no great difference in the number of pairs of cases in the two sexes. These generative organs are without outlets, the germinal products escaping from them, when fully ripe, by the dehiscence or bursting of the walls of the capsule and the lining membrane of the cavity, and thus get into the branchium from whence they pass into the surrounding water, the spermatozoa to come in contact with and impregnate the ova, and the ova to develop into young animals.

This escape from the body is probably effected during the feeding time of the animals, when there is a current more or less strong passing through the branchium. The exact method by which the ova become impregnated is not known, but it may be supposed that the spermatozoa, after passing from the male, move about in the water until swallowed by a feeding female, when they pass into the branchium with the greater quantity of the water, and so get to the cases containing the ova, penetrate the capsules, or more likely adhere to the exterior until the ova are extruded, and then effect the work of impregnation. Any ova which were in the branchium at the time of the entrance of the spermatozoa, and which had been recently separated from the cases, would of course be very quickly fastened upon and impregnated.[1] Each ovary, if a single case may be considered to represent an ovary, contains from twenty-five to thirty ova, and each ovum is enclosed in a separate membrane or cell, any one of which may open and discharge its contents without affecting the rest of the case. Under the microscope these cases appear like small bags of marbles or bunches of grapes, except that most of the ova show a lighter, roundish spot near the center, which represents a nucleus, the nucleolus not being visible (Fig. 4, Pl. II). After escaping from the cases and becoming free in the branchium, the ova in all probability, pass out of the body, by way of the branchiopore, in the water which is being constantly expelled from this orifice during the process of feeding. Up to 1873 this was considered, by careful observers to be the only method by which the ova could possibly escape into the surrounding medium, and Quatrefages says that he saw them, under the microscope, pass from this aperture. But Kowalevsky, in his paper upon the development of Amphioxus,[1] says that *he* saw the eggs issue from the *mouth* of the female in bunches of fifteen or twenty, and hence concludes that they are normally extruded from this opening. This abnormal proceeding on the part of Amphioxus has been questioned by Wm. Müller[2] on the grounds that the branchial slits are too narrow to admit of the passage of the ova in this direction, and Prof. Huxley seems to be of the opinion[3] that if this proceeding took place as described by Kowalevsky, that it was accidental, and due to some of the ova in passing out by the branchiopore getting caught in the openings of the lateral folds, being carried along the hollows of these folds and discharged at their anterior openings into the mouth cavity and thence out of the body. But this would not account for their issuing in bunches of fifteen or twenty, and moreover, as there are no such openings to the metapleura (ante p. 6), the ova could not have passed in this direction. Prof. Ray Lankester[4] sides with Kowalevsky, and says that in all probability the ova *do* pass from the mouth, but if not by the branchial slits, then by certain openings which exist, one upon either side, and connect the branchium with the buccal cavity. This connection has not been noticed by previous observers, although Prof. Lankester thinks that these openings are the ones figured by Joh. Müller[5] and considered by him to be the anterior openings of the meta-pleura. In the case of the female which was in my possession, the ova were extruded very gradually and for the most part one by one, so that here and there along the row of cases could be seen, one with a single ovum gone, others, nearer the ends, half empty, and still others, near the middle, with their full quota. During this period, which extended over the entire time the animal remained alive, I was not fortunate enough to see any ova leave the body, but from the size of the branchial slits, the position of the generative bodies, and the actions of the cilia, currents and abdominal walls, which I studied with considerable care, I arrived at the conclusion, which is in accordance with the opinions of Wm. Müller, Quatrefages, &c., that, the ova all passed from the body by the branchiopore, and that while not absolutely impossible, it would be an exceedingly exceptional proceeding if any should pass out by way of the mouth. I found that seven ova placed side by side extended over a space just equal in length to the breadth of five branchial slits with their enclosing arches, and as the bars of the arches are quite as broad as the slits, the ova in passing out in this direction would be obliged to pass in opposition to the powerful action of the branchial cilia and inflowing water, through openings which at most would be only seven-elevenths as broad as the diameter of a single ovum, which would be an exceedingly difficult performance. If the openings mentioned by Prof. Lankester exist, and are no broader than the breadth of the branchial slits, there would be the same difficulty in passing through them as in forcing a way through the slits, besides having to traverse nearly half the length of the pharynx against the current of water and the pressure of the abdominal walls. If these openings are larger than the openings of the slits, it would hardly seem possible that they could have remained undetected until this late date, but even in this case the passage of ova through them could hardly be more than an occasional and chance occurrence, since the same obstacles exist to the passage of the ova forward to these openings as in the case of the smaller ones, and are even increased by the liability of currents of water setting through them into the branchium and thus assisting in expelling the ova by the branchiopore. Thus in any case there would be great difficulty for the ova to get *into* the mouth cavity, and when once in they would be fully as liable to be drawn down through the pharynx into the stomach as to be expelled from the body. But it seems to me that it is not necessary to suppose any such difficult and abnormal passage, as it appears possible to harmonize, in a natural manner, the opposing views of Kowalevsky with those of Quatrefages and Wm. Müller, for *apparently* the ova *may* proceed from the mouth, while *actually* they make their exit from the branchiopore. When we consider the position of Amphioxus during feeding time, that is, when it comes to the surface of the sand, we find that it has formed for itself a sort of sand tube in which it lies, belly upwards, with its mouth orifice, or a small portion of its body exposed to view, as it was when Kowalevsky saw the ova issue. Now at every contraction of the abdominal walls there will be left a space between the body and sand, extending from the branchiopore to the mouth, or near it, through which the water expelled from the branchium may pass to and mingle with the water above the sand. And if at this time the ova are extruded from the pore along with the water, they will naturally rise to the surface of the sand, pass along by the mouth tentacles, *appearing* to any but the most careful observation *to come from between them*, and so into the medium where they float about until transformed into young Amphioxi. If this is the true method of procedure, as it is the most simple and natural, it will account, *as no other method will*, for the little bunches of fifteen or twenty which Kowalevsky saw emerge into the water. For in passing from the pore out against the sand it would be very easy for some of the ova to become lodged against the sides of the tube until a number of them accumulating together would form an obstacle of sufficient importance to be forced out by the outflowing water, and sent along by the tentacles, when they would be seen rising in the water as if just escaped from the mouth cavity.

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[1] It is possible that it may be shown hereafter that the ova are impregnated only after they pass from the female into the surrounding water, there meeting the floating spermatozoa which have been discharged from the male.

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[1] Entwicklungsgeschichte des *Amphioxus lanceolatus*. Von Dr. A. Kowalevsky, Mem. de l'Acad. Imp. des Sciences de St. Petersbourg, VII^{me} série. Tome XI, No. 4, p. 1. St. Petersburg, 1867.

[2] Ueber das Urogenital system des Amphioxus, &c. Jenaische Zeitschrift, Vol. IX, p. 94. 1875.

[3] Classification of the Animal Kingdom. Prof. T. H. Huxley. Quar. Jour. Microscop. Sci., Vol. 15, p. 54. 1875.

[4] Loc. cit., p. 263.

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[5] Ueber den Bau und die Lebenserscheinungen des *Branchiostoma lubricum*. Von Joh. Müller. Abhandlungen der Berliner Akad. Berlin, 1842 (1844), Pl. III, Fig. 4, *e*.

The Urinary System.—The earlier anatomists who examined Amphioxus were unable to discover any organ, or series of organs, which could be considered as acting as specialized excretory vessels for the urinary products, and for quite a time it was a matter of considerable speculation as to the method by which these products, if any were formed, were eliminated from the body. Very soon, however, certain isolated, ductless, glandular patches were discovered to exist upon the floor of the posterior portion of the branchium near the branchiopore, and as no other function could be thought of as being performed by them, and as there were, apparently, no other organs which might subserve the purposes of excretion, it was supposed that these patches acted in this capacity, and after eliminating the urinary products cast them into the branchium to be extruded from the body through the branchiopore with the water which passed from this orifice.

This opinion, which might be considered as very plausible, since the patches were associated in position with the posterior generative bodies, was very generally held until quite recently, but in the paper by Prof. Lankester, already referred to, he announces the discovery of certain canals which he considers as representing, rather than these patches, the true urinary ducts of Amphioxus. These vessels, one upon either side, are in the form of long tubular ridges, formed along the roof of the pleuroperitoneal portion of the branchium as outgrowths from the mesoderm of the body walls. They are composed of pigmented cells and their posterior extremities are open and communicate with the branchium near the branchiopore, but their anterior extremities, which are in the neighborhood of the sides of the pharynx, are probably closed. These canals are thus apparently homologous with the earlier stages at least of the ducts of the uriniferous tubules of other vertebrates, and unless further investigation shows them to appertain unmistakably to some other system they will undoubtedly henceforth be considered as representing, as Prof. Lankester suggests, the urinary system of this animal.

The Blood Vessels.—The general arrangement of the vessels of the blood system in Amphioxus is very similar to that found in the young of all osseous fishes, but in the minutiæ of the plan there are quite important modifications, which, although not making a complicated system, yet render it very different from any other known among vertebrates. The main blood vessel, or vein, extends from the anus along the ventral aspect of the intestine to the base of the saccular liver, thence around the entire length of this organ upon both ventral and dorsal edges, to continue along the ventral aspect of the œsophagus and pharynx to a point just beneath the first branchial cleft where it expands or merges into a bulbous organ, the heart. This canal is pulsatile, and has been given different names according to the section of the body through which it passes, but it is undoubtedly to be considered as a single vessel, since it is of nearly uniform calibre throughout its course, and the rythmical contractions, which are a very marked feature and readily seen, especially in the young, pass from behind forwards, at somewhat lengthy intervals, along its entire length. Up to quite recently this long tubular vena cava was considered to be the sole pulsatile organ of Amphioxus, and as a "tubular heart," which was the term applied to it, was an anomaly among vertebrates, it was thought fit to designate the "thin" from the "thick" hearted vertebrata, and thus separate Amphioxus from the rest of the family by instituting for its sole reception the class Leptocardia. But in 1876 Langerhans announced[1] the discovery of the organ, which is described above, as being situated at the anterior extremity of the vena cava, and which he considers as representing the heart. If this is the case, and Amphioxus does indeed possess a thick-walled pulsatile cavity, the above classification may have to be revised, but even then the pulsatile character of the vena cava, together with the other peculiarities in the organization of Amphioxus, may be considered of sufficient importance to make it the unique representative of a distinct class. From each side of the pharyngeal portion of the vena cava a series of vessels are given off, which correspond in number and position to the main bars of the branchial arches, and through which these vessels pass to the dorsal edge of the pharynx, where they unite into two aortæ, which run back without any intercommunication, one upon either side of the median line, to the œsophagus, where they unite into a single tube, which proceeds as a distributing vessel to the end of the body. Each series of these branchial or blood-renovating vessels forms its own aorta, and each individual vessel has, at its base or origin, a small dilatation or bulb-like enlargement to which the name of "branchial heart" has been given. These "hearts" lie in the alternating triangular spaces between the curved bases of the cartilaginous arches, *a*, Fig. 4, Pl. 1, and probably act as elastic reservoirs to render the flow of blood steady and continuous through the branchiæ. The main heart, into which a certain, perhaps a large proportion of blood from the vena cava passes, gives off three vessels, two small ones from its anterior border, and a large one from its left side. The anterior vessels proceed to and supply the walls of the buccal cavity and the tentacles, and the left branch, which forms the ductus Botalli, or aortic arc, passes across the pharynx between the pharyngeal ring and the anterior branchial clefts, to unite with the left aorta, formed by the union of the left branchial vessels, and by this route sends its blood into the main arterial channel.

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[1] Zur Anatomie des *Amphioxus lanceolatus*. Von Dr. Paul Langerhans. Archiv für Mikrokopische Anatomie. Band 12, p. 336, fig. 49*c*. Bonn, 1876.

The blood of Amphioxus is colorless, containing only white nucleated corpuscles,[1] and very few of these. The manner, however, of its distribution from the aorta and branches of the heart to the different parts of the body and its return to the vena cava and heart is not at present known. It may be that the passage is effected by means of capillary vessels which are so minute that they have not as yet been made out, or it may be, and which is much more probable, that this fluid passes through the interspaces between the various tissues, or in other words, that the large blood vessels terminate as blood sinuses.

Development.—For those changes which take place in the embryo of Amphioxus previous to the formation of the side folds, and for most of my information in regard to the growth of these folds, I am chiefly indebted to the investigations of Kowalevsky[2] who has shown that shortly after the impregnated ovum leaves the branchium of the female and passes into the surrounding water, the granular vitellus, which nearly fills the rather delicate vitelline membrane, undergoes complete segmentation and gradually builds up a thin-walled, nearly spherical morula, which soon, under the energetic action of the numerous external vibratile cilia, each cell of the wall being furnished with one or more of these little lashes, begins rolling over and over, quite slowly, within the enclosing membrane, agreeing in this respect with what is seen in the ova of certain other vertebrates and many of the invertebrata. After the commencement of these rotary movements, or it may be before they begin, the morula becomes transformed, by the introversion of one side and the subsequent near approximation of the edges of the cup thus produced, into a gastrula, and the gastrula, by the elongation of its

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[1] Examination of the corpuscles of the blood of *Amphioxus lanceolatus*. Prof. T. H. Huxley. Report of Brit. Ass. of Science. London, 1847. Report of sections, p. 95.

[2] Loc. cit. and Weitere Studien über die entwickelungsgeschichte des *Amphioxus lanceolatus*. Archiv. für Mik. Anatomie, XIII, p. 181. Bonn, 1877.

sides in the direction of the axis which passes through the gastrula mouth, or blastopore, changes into a slender, compressed, double-walled, planula-like body, ciliated within and without, and with the two walls, or exoderm and endoderm layers, which surround the rather large central cavity of invagination, lying close together one within the other, but separated by a narrow space which represents the remains of the original segmentation cavity of the morula. By the time the embryo is well established in its planula form, the blastopore, which marks the posterior extremity of the body, closes up entirely, or at least it is highly probable that it does, and the young Amphioxus escapes from its shell and becomes a free swimming inhabitant of the water. The cells of the exoderm and endoderm, along one edge of the embryo, now become longer and larger, entirely obliterating in their growth the segmentation cavity in this part of the body, and form between them, throughout the length of the animal, a strip of mesoderm in the center of which arises the notochord and from the sides of which originate the muscle plates of the body muscles. As the mesoderm thickens, two longitudinal ridges grow up from the exoderm and, arching over, unite upon the median line into a dorsal tube which runs parallel with and close above the notochord. Within this tube the central portion of the nervous system is formed. This arises as a second tube lining the walls of the first, and originates from the differentiation of the exoderm cells of the latter. During its formation the ends of the dorsal canal have been gradually closing up, one of them, the posterior, completely, and the other, the anterior, all except a narrow outlet which persists until a somewhat later stage of development.

Meanwhile the whole body lengthens; the exoderm of the ends stretches away from the endoderm into thin blade-like points; the central cavity, limited by the transformation of the dorsum to the lower half of the body, becomes long and tube-like posteriorly, and quite broad throughout its anterior third; a welt or pear-shaped body, with the narrow end pointing downwards, forms across the anterior end of this broad pharyngeal portion of the central cavity, and the external cilia, which heretofore have been the sole motive power, supplanted in their functions by the muscular fibres of the mesoderm, disappear, except upon a small depressed pit-like bit of surface situated upon the left side of the anterior end, a short distance back from the extreme point of the body. The middle part of the tubular portion of the central cavity now enlarges into a small oblong stomach, with obliquely-placed cilia along its walls, and openings, formed by ingrowths of cells from the exoderm, appear upon the left side of the body, one at either end, placing the central cavity in communication with the exterior. The posterior of these openings is formed at the very extremity of the cavity, at the base of the exodermic tail expansion, and at or near the point of closure of the blastopore, and it may be that it is rather a reopening of the old gastrula mouth than a new formation, although the latter seems to be the opinion at present.[1] It is small, slightly dilatable, and becomes the anal aperture of the intestine. The anterior opening penetrates the body wall along the anterior half of the pharyngeal portion of the cavity and becomes the mouth orifice. It is at first a short longitudinal slit, but soon broadens into an oval aperture of considerable size, with long, slender, alternating, teeth-like processes extending out from the edges towards the center as guards to the entrance, and a thickening of the body wall takes place just below it, forming a prominent ridge-like border extending from near the median line below the cartilaginous, pear-shaped welt, backwards and upwards to very nearly the level of the notochord. Along the inner, lower edge of this mouth-ridge there are generally two or three slender pointed processes which lie close to the body and point towards the right side. The central cavity is thus at once transformed into a digestive tract, the food particles being drawn in at the mouth by the action of the internal cilia, passed on to the stomach, where they are twisted and ground up for the nutrition of the animal, and the refuse material sent onward to the anus and so out of the body.

A third opening now makes its appearance, piercing the body wall upon the median ventral line just below the mouth orifice. It is somewhat larger than the anal opening, longer than broad, with the longer diameter transverse to the length of the body, and forms the first of a series of ten or eleven similar pharyngeal clefts which open along the under side of the pharynx at regular distances back to very near the middle of the body. Coincident with the formation of this first pharyngeal cleft, two delicate

[1] Early stages in the development of Vertebrates. F. M. Balfour. Quar. Jour. Mic. Science. Vol. xv, p. 208. Camb., 1875.

longitudinal folds arise from the exoderm along either side of the entire length of the upper portion of the central cavity, and grow outward and downward toward the ventral aspect of the body. They soon attain a level with the lower edge of the intestine, which, as already mentioned, is much narrower than the pharyngeal section, and those portions of the folds which lie along the intestine closely embrace it as a sort of tubular outer coating, and unite along their edges into a broad median ridge which extends from the anus, where it merges into the exodermic tail expansion, to a point just in front of the stomachic dilatation. This ridge forms the ventral extension of the continuous ventro-dorsal median fin.

The anterior portions of the folds now increase in breadth, leaving quite a space, the rudiments of the branchium, between their edges and the alimentary tract, and gradually unite but with a smooth, unridged surface, along the median line forward toward their anterior extremities. In this union an opening is left between the edges of the folds just at the point where they leave the anterior edge of the coalesced ventral ridge; this opening, which forms a means of communication between the cavity enclosed by the folds and the exterior, represents the abdominal pore, or branchiopore. It will thus be seen that the abdominal portion of the animal presents two widely different sections; the one, posterior, with firm walls, closely surrounding the intestine and stomach, and with a very restricted cavity enclosed between the body walls and this portion of the digestive apparatus; and the other, anterior, with thin dilatable walls, which are at some distance from the alimentary tract and which enclose quite an extensive cavity or space, which communicates directly with the exterior and with the cavity of the posterior section. It may be that these two sections are somewhat more complicated in their formation than I have indicated above, that while the posterior portion is fashioned as already mentioned, the walls of the anterior cavity are formed by the outgrowth of new folds from the inner edges of the old ones; that is, that after the coalescence of the posterior portions of the first folds around the intestine, these folds grow no further, but a new set originate from the inner anterior borders of the first, and by the extension and subsequent union of these more delicate laminæ, the walls of the anterior cavity are formed. The peculiar pit-like character of the branchioporic depression would seem to indicate some such development, and in this case the lateral abdominal folds, the metapleura of the adult, would represent the external edges of the first pair of reduplications. This point will, however, be rather difficult to ascertain, and I am obliged to say that in none of my young specimens did I see any direct evidence of any such secondary growths, the development appearing to be as first described, so that I shall continue to consider the cavities as formed only of two folds. In whichever manner, however, they are formed, the one slender and of little account, being barely discernible, the other large and of great importance in the animal's economy, they are both lined, from the nature of their formation, with a continuous layer of exoderm, that upon the external walls of the cavities being derived by cell multiplication directly from that which covers the inner walls. At this period the right fold extends forward as far as the edge of the cartilaginous welt, where it merges into the exoderm, the left, as yet, only to and uniting with the edge of the mouth ridge, both being perfectly free from the sides or lower edge of the pharynx, and by the time they have united along their ventral edges to a short distance in front of the branchiopore, two or three additional pharyngeal clefts have formed along the median line of the pharynx, and the animal now appears much as shown in Fig. 7, Pl. II, which represents the youngest of the specimens which came into my possession. Here can be seen the long notochord with the slender, tubular, spinal axis above it; the ciliated pit just in front of the pear-shaped welt; the side mouth with its teeth or tentacles; the cilia lining the alimentary tract; the long œsophagus, the dilatation for the stomach and the asymetrical anus forced to one side by the outgrowth of the exoderm of the tail and the median ridge of the ventral folds; the depression indicating the position of the branchiopore; the three pharyngeal clefts piercing the pharynx beneath the mouth aperture, and the long tubular heart, formed at about this period, between the endoderm and exoderm of the ventral edge of the alimentary tract. The shape of the animal is quite characteristic, very much compressed from side to side and pointed at either extremity, but the posterior end is not often knobbed, as shown in the plate, having generally the shape shown in Fig. 5, Pl. I. The full number of clefts now soon appear along the lower edge of the pharynx between the open edges of the side folds, and, about the time of the formation of the last cleft, the mouth aperture begins to change its position, moving forward very slowly toward the cartilaginous welt and the ciliated pit. Accompanying this forward movement of the mouth the anterior pharyngeal clefts become pushed over toward the right side of the pharynx, and to a slight extent under the right fold; the posterior part of the ciliated pit grows backward, burrowing into the tissue toward the cartilaginous welt; and the cartilaginous welt broadens throughout its upper portion, the upper posterior limb growing backward towards the mouth, and a slit or opening forms through its center so as to transform it into an irregular pear-shaped ring of cartilage placed obliquely across the anterior portion of the central cavity. Fig. 5, Pl. II, represents a diagrammatic cross-section of the body at this stage of growth. The section is made transversely through the mouth and one of the pharyngeal clefts, as at *a*, Fig. 7, Pl. II. The mouth opening, with its teeth-like processes, is seen upon the right side; the mouth *welt* with *its* processes below it; the pharyngeal cleft pushed just to the left of the median ventral line; and still further to the left a slight indication of the anterior portion of the right body fold. The mouth and pharyngeal apertures open directly into the digestive tract.

The forward movement of the mouth, and the backward movement of the ciliated pit, continue until the anterior edge of the mouth aperture is close to the posterior limb of the cartilaginous ring, and the posterior portion of the ciliated pit has burrowed back to the opening in the ring, when a split takes place in the body wall extending from the mouth opening forward over the the edge of the cartilaginous welt and through into the ciliated pit, Fig. 2, Pl. II, in which only the edge of the ciliated pit is indicated, the central, deeper portion being back towards the central dotted lines of the figure. This split now deepens or extends to the center of the pit, forming a passage-way into the digestive tract through the cartilaginous ring; the mouth aperture and split in the body wall gradually close; the bottom of the ciliated pit becomes attached to the edge of the cartilaginous ring, which is already attached to the walls of the anterior extremity of the pharynx, and the food passes into the digestive tract from this time forward by way of the newly opened aperture in the bottom of the ciliated pit. This is a marked advance in development, and it is hardly more than accomplished, and perhaps in many instances not completed, before the body folds close up entirely over the pharyngeal clefts, the left body-fold advancing towards the cartilaginous ring coincident with the advance and final disappearance of the pharyngeal mouth aperture and mouth welt; the first two or three pharyngeal clefts become pushed almost entirely over upon the right side of the pharynx; the ciliated mouth cavity enlarges anteriorly, the dorsal and posterior edges growing downward and forward, and small fleshy prolongations appear upon the posterior edge; and two or three small oval openings appear piercing the left side of the pharynx at points intermediate to the already formed pharyngeal openings, in a line just posterior to the cartilaginous ring and beneath the level of the notochord. Fig. 1, Pl. II, shows the appearance of the anterior portion of the animal at this time, with mouth tentacles beginning to show along the posterior edge of the cavity, and the oblong openings along the left side of the pharynx.

These openings in the pharynx represent the rudiments of the left branchial fissures or arches. They increase in size until the first one is about one-half the width of the pharynx, when a small protuberance forms in the center of the upper or dorsal border, and grows downward towards the ventral edge, finally merging with it and dividing the opening into two more or less elongated apertures, the branchial slits or clefts. Before this division is effected however, each of the other openings has given rise to a central prolongation, which grows downward to finally unite with the lower border, as in the first case, and two or three new openings have pierced the pharynx, one between the first arch and the cartilaginous ring, and the other in a line with, and posterior to, those first formed in the pharyngeal wall.

Of these new arches, the first one never becomes divided by a central bar, but each of the others is divided in turn into two sections, as a new opening makes its appearance in the pharyngeal walls. As there appears to be no limit to this formation of arches, and of their division into clefts, in the growth of the individual, there is always to be seen in either young or adult, a posterior round or oval aperture and just anterior to it one or more openings partially segmented by central prolongations, although sometimes the last aperture indicates the central division, by a curvature of the dorsal edge, before the new opening is formed. After the segmentation of the arches, each bar becomes itself divided, in time, into two halves, or at least marked, as seen in the adult, by a distinct central line of division, Fig. 4, Pl. 1. In all of the arches a circlet of long cilia appear around the inner edge as soon as the aperture is formed, and, with the growth of the central bars, the circlet gradually extends so as in the adult to nearly if not quite curtain each cleft, and when in motion form such admirable strainers for these openings, as has been indicated when speaking of the habits of these animals. The movement of the cilia is wave-like and continuous around the edge of the slit, with the *stress* or *emphasis* of the motion always in the same direction.

In the meantime, while the left branchial arches have been enlarging and dividing, the first three or four pharyngeal openings have attained a counterbalancing position upon the right side, and have, similar to those of the left side, become divided into branchial slits by the downward growth of central bars, and the remaining pharyngeal openings have entirely disappeared, so that at this period both sides are pierced by ten to twelve similar alternating clefts, the first one of the right side being formed like the corresponding one of the left side, after one or two of the old apertures have become divided into clefts, although it is possible that in some instances this first slit may be the first pharyngeal opening, which has remained small and undivided, merely increasing slightly in length in the direction of the breadth of the pharynx, with the general increase in length of the other clefts. The subsequent arches of the right side are of similar formation to those of the left, that is, they are new openings, which are formed through the wall of the pharynx, and in all probability none of them have any relation to the five or six pharyngeal openings which closed up during the changes of the first three or four. Accompanying these modificatiens which take place in the arches, there is an enlargement of the ventral portion of the center of the alimentary tract, and a forward movement of the stomach, so that this organ comes finally to lie within the enlarged anterior cavity of the abdomen, rather than within that portion closely embraced by the side walls.

The enlargement of the alimentary tract is, at first, in the form of a mere swelling-out of one side, accompanied by a pigmentation of the cells of the walls of this section of the tract, but, in a short time a diverticulum, with greenish walls is formed, which grows forward (Fig. 3, Pl. II), gradually pushes its way along the side of the pharynx (Fig. 3, Pl. I), and becomes the asymetrical liver of the adult.

As the liver passes forward around and along one side of the pharynx, that portion of the ventral tubular vessel of the blood system which passed beneath it becomes stretched out into a peripheral ventral and dorsal vessel for this organ, so that there is, so far as can be made out, no connection between the intestinal and pharyngeal portions of the ventral vessel, except by way of this extension which outlines the liver. In Fig. 5, Pl. I, the liver enlargement is represented at about the time it begins to form, and the ventral vessel is seen to conform to the outline of its lower edge.

A second vessel is also represented, which first appears about this time, extending from the cartilaginous base of the pharynx, between the branchial arches and the pharyngeal ring, upwards and backwards to the ventral aspect of the notochord, where it becomes lost to view. This vessel is the aortic arc or ductus Botalli, and with the exception of this arc and the ventral vessel, with its hepatic continuation and the swellings at the bases of the branchial arches, no portion of the blood system can be made out in the living, young or adult animal. At this period the branchial arches are seven in number upon either side of the pharynx, the third and fourth from the anterior end being largest, and are very broad and well defined, with very large spaces between their broadly pointed bases, and the stomach is seen just over the branchioporic depression, and extends forward into the enlargement caused by the swelling-out of the alimentary tract for the liver cæcum, and in fact this enlargement, and also this section of the alimentary tract after the farther growth of the liver, seems to form a very important part of the stomach, and the swaying, twisting mass of food, with the accompanying oblique arrangement of the cilia, generally extends from the posterior limits of the œsophagus to the beginning of the intestine. The advanced state of the mouth cavity and the tentacles upon the pharyngeal ring will also be noticed in this figure. From the condition as shown in Fig, I, Pl. II, the posterio-dorsal, or left, and the ventral, or right edges of the mouth cavity gradually work downward and forward until the ventral edge nearly coincides with the ventral edges of the anterior portion of the body, by which time this edge has become lip-like and three or four finger-like prolongations have formed from the exoderm of the lip.

At the same time with the forward growth of the left side wall, the tentacles of the left side have grown longer, increased in number by the addition of one or two prolongations from that portion of the wall of the cavity anterior to those tentacles already formed, and become strengthened by cartilaginous supports formed in the tissue of each tentacle, as tentacular segments, already noticed in the adult, of the left branch of a ring which develops around the edge of the mouth aperture from the base of the cartilaginous ring of the pharynx.

At this period the mouth tentacles have very little share in guarding the mouth cavity from the entrance of large or injurious particles, this duty being delegated almost entirely to the tentacles of the pharyngeal ring, which were formed very soon after the opening of the passage-way through the bottom of the ciliated pit into the pharynx. And while these pharyngeal tentacles are thus of much greater importance to the young than to the adult animal, they are always of service, as has been noticed upon a previous page, in ejecting large bodies which may have succeeded in passing the network formed by the mouth circlet and getting into the mouth cavity. The further development of the mouth cavity is comparatively simple; the left side continues its downward and forward growth, until it is upon a level with the right edge, and the mouth opening becomes a median, ventral aperture just posterior to, and guarded by the rather blunt proboscis of the animal; the right branch of the mouth ring with *its* segments, forms in and along the edge of the right wall, and the cartilaginous supports grow out into the right tentacles; the remaining tentacles, to the number of ten or eleven on either side, making about thirty-one in all, gradually form along the sides, arching inward and forward, so that those of one side overlap and interlace with those of the other, and the mouth cavity assumes its normal adult appearance (Fig. 1, Pl. 1).

By following carefully the development of the mouth cavity of Amphioxus, as I have sketched it in the previous pages, it will be seen to be a true, although somewhat irregular, introversion or inward growth of the exodermic tissue to meet the endoderm of the central canal, and hence is homologous in character with the mouth cavity of the higher vertebrates. It has heretofore been generally considered that the mouth cavity of Amphioxus was formed by the anterior portions of the side folds overlapping and finally enclosing the anterior end of the pharynx, and by this method of development making the mouth cavity an anterior portion of the cavity surrounding the pharynx. But in none of my specimens could any evidences of any such method of formation be seen, and there are, moreover, certain facts in connection with the formation of the mouth cavity which would seem of themselves to corroborate, to a certain extent at least, my view of the development. First, the mouth being formed upon the left side of the body, has, in the anterior exodermic expansion, a previously-formed right wall, and any extension of the right fold over this portion of the body would only form a third layer over the side and not be of any value in the formation of the cavity, or connect it in any manner with the cavity surrounding the pharynx. Second, the left fold, in order to form the left side of the cavity would have to pass forward over the pharyngeal mouth aperture, and in so doing would so affect the inward flow of food material that this forward growth could be easily observed, provided any such forward growth took place. But the left fold is always limited anteriorly, so far as I have observed, by the mouth welt, and advances towards the cartilaginous ring only as the mouth welt advances towards the edge of the ciliated pit, hence my investigations have led me to the conclusion already mentioned, that the mouth cavity is formed by a true introversion of the exoderm, and is genetically distinct from the branchial cavity. For this reason, combined with the fact that the branchial cavity is essentially branchial in its function, and quite different in its formation from the atrium of some at least[1] of the Tunicates, its walls having more of the nature, in their development, of the gill covers or opercula of osseous fishes,[2] and because it does not function as a cloacal chamber, although indeed receiving the urinary and generative products, I have thought it best to give it the name of branchium rather than that of atrium, which is applied to the branchio-cloacal chamber of Tunicates.

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[1] The Anatomy of Invertebrated Animals. By T. H. Huxley. London, 1877, p. 609.

[2] To indicate my meaning as to the homology of the branchium, I would say that if those portions of the side folds, which by their union form the median ventral fin, should be extended forward to a point along the œsophagus, and by their union or coalescense at this point completely cut off the posterior from the anterior cavity; and the ducts of the uriniferous ridges should extend back to the anus, where they could open into a cloaca, and the generative products instead of bursting through the lining of the walls into the branchium, be carried back between the lining and the muscles to the cloaca and there discharged, or in other words, if the pleuro-peritoneal cavities of the roof of the branchium should become more enlarged in the pos-

The changes which take place in the nervous system while these transformations are taking place in the muscular system and integument, appertain chiefly to the growth and extension of the nerves out into the parts of the body from the chorda spinalis. The chorda itself changes very little in the growth of the animal from what it was in the embryo; the principal difference being that in the adult the central canal has become almost completely filled up, except in the "head," by the thickening of the walls, and the pigment spots are perhaps somewhat larger and more numerous. The posterior extremity is turned up very slightly from a very early period, but it does not exhibit the button-like termination until later in life. The anterior end, or "head," enlarges somewhat in the growth of the animal, so as to represent a very rudimentary brain, and the beak of the "head" and the olfactory nerve attain their adult characteristics probably coincidentally with the outward extension of the peripheral portion of the nervous system, or the general body nerves.

The farther development of Amphioxus has already been indicated in the forward growth of the liver, the multiplication and elongation of the branchial slits, the outgrowth of the ventral cartilaginous processes, forming a base to the ventral median fin, and the extension of the muscle plates down into the body walls.

With these transformations are associated certain changes in external form, particularly in regard to the shape of the two extremities and the appearance of the metapleura of the side folds, and when these are accomplished, the animal has assumed its adult form, as represented in Fig. 1, Pl. 1, and with the development of the generative bodies along the edges of the muscle plates, becomes capable of reproducing its kind.

In conclusion, it may not be unprofitable to summarize, somewhat hastily, those particular features in which Amphioxus dif-

terior portion of the animal, and while extending to the cloaca and opening there, include in their cavities the reproductive organs, then this posterior cavity would represent a true perivisceral cavity or chizocœle. In this case the anterior portion of the folds, forming after the posterior portions, and either from them or in front of them, would be true opercula covering the branchiæ, and it is possible that the growth or formation of the body cavity and opercula in vertebrates has been along some such line of development.

fers from other vertebrates. Beginning with the external characteristics we find a median ventral fin, which is continuous with a long median caudo-dorsal fin, extends for some distance in front of the anal aperture, and which extends quite to the anterior extremity of the body; an anal aperture placed upon the left side of the median line of the body and opening about midway of the side; an abdominal aperture or branchiopore; a longitudinal mouth opening; a circlet of mouth tentacles; and a single asymmetrical nasal pouch. It is very questionable whether the anterior pigment-spot of the spinal cord is of any more value than any of the other pigment spots of the nervous system, hence Amphioxus may be said to absolutely lack both eyes and ears.

Internally we find a saccular liver; and an alimentary tract lined with vibratile cilia. The notochord, besides lacking any anterior cranial expansion, may differ in its structure and mode of development from the notochord of higher vertebrates, but this question is as yet undecided. The remaining organs represent rather embryonic forms of the same organs in higher animals, than different features; thus the spinal cord, with its slight anterior enlargement seems to represent that stage of the central nervous system of higher vertebrates just before the cerebral vesicles are formed; and the blood system, if, as Langerhans claims, there is a heart, and if the blood is distributed throughout the body and returned to the ventral tubular vessel through the spaces in the tissues, rather than through capillary vessels, would be, excepting the position of the heart and the pulsatile character of the vena cava, simply what is seen in all young vertebrates, or at least as seen in the young of osseous fishes, where the course of the blood in the smaller channels is continually changing from one interspace to another, whenever, from any cause, any one channel becomes stopped up, and these changes continue until the capillary vessels are formed. Amphioxus is thus seen to be a *very* peculiar animal, presenting some resemblance to the Tunicates in the ciliated pharynx and pharyngeal tentacles, yet evidently more closely affiliated as an embryonic form, with the great vertebrate branch of the animal kingdom, than with any of the Invertebrata.